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Bureau of Plant Industry
U. S. Department of Agriculture,
Cooperating

8 JUN. 1923
OF MYCOLOGY

RESEARCH BULLETIN NO. 72
JANUARY, 1922
AMES, IOWA

January, 1922 Research Bulletin No. 72

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By I. E. MELHUS, S. M. DIETZ AND FLORENCE WILLEY

In a further study of the crown rust problem and its control, it became necessary to consider its alternate hosts and biologic specialization. Altho these phases have received extensive investigation in Europe by de Bary (5), Eriksson (10), (11), (12), Klebahn (24), (25), (26), (27), (28), and others, yet they have scarcely been considered in America. On purely theoretical grounds, it would be unusual to expect the same conditions to exist in America, where there are different species of Rhamnus and grasses, as well as different climatic and environmental conditions. In fact, enough work has already been done by Carleton (7), (8), Arthur (2), (3), (4), and Melhus and Durrell (29), on the relation of crown rust to Rhamnus and on biologic specialization, to indicate clearly that the results in America should be different.

The investigation reported in this bulletin deals with the most common grass hosts of crown rust in oat growing sections, *Avena sativa, Calamagrostis canadensis, Festuca elatior, Lolium perenne* and *Holcus lanatus,* together with seven native and two introduced species of Rhamnus, used as alternate hosts. The data presented is discussed in two chapters, namely, alternate hosts and biologic specialization.

I. THE ALTERNATE HOSTS OF PUCCINIA CORONATA CORDA

In Europe crown rust (*Puccinia coronata* Corda) has been divided into two species, *P. coronata* and *P. coronifera,* by Klebahn (24). Eriksson (10) later divides these two species into four series, as follows: Series I. Aecidium on *Rhamnus cathartica, (Rh. elaeoides, R. grandifolia, R. alnifolia), (Puccinia coronifera* Kleb.) Series II. Aecidium on *Rhamnus frangula* (*Puccinia coronata* Corda Kleb.) Series III. Aecidium on *Rhamnus dahurica* (*Puccinia coronata* var. *himalensis* Barcl.) Series IV. Aecidium unknown, uredospore stage on *Melica nutans.* The chief distinguishing characteristic is based on the different species of Rhamnus used as alternate hosts. In other words, the species concept is largely based on biologic, rather than on morphologic differences. Since comparatively little work has been done on the alternate hosts of crown rust in America, it is not known to what extent it is justifiable to follow the results of European workers.

This chapter reports studies on the relation of the most important Rhamnus hosts to crown rust as it occurs on *Avena sativa, Calamagrostis canadensis* and *Festuca elatior.*

*MS. transmitted to Director Jan. 9, 1922. Approved for publication Jan. 12, 1922.

Among the first problems that arose in studying the alternate hosts of crown rust on oats and the two above named grasses, were those of the distribution and susceptibility of species of Rhamnus. Their solution has involved a study of two European and seven native species. The European literature has been admirably reviewed by Klebahn (24), (25), (26), (27), (28), Eriksson (10), (11), (12), and Mühlethaler (30), (31), on Rhamnus as an alternate host for crown rust and there is no need for the discussion here. American literature, however, should be reviewed.

Among the American writers, Arthur and Holway (1) were the first to study the relation of Rhamnus species to crown rust. In 1898 aecidiospores from *R. lanceolata* were placed on *Avena sativa,* which resulted in sori appearing on the oat seedlings eight days later.

Carleton (8) later worked with aecidiospores from *Rhamnus lanceolata* and was able to produce uredospore sori on *Phalaris caroliniana.*

Following close upon the work of Carleton, Arthur in 1905 (2) found that aecidiospores from *Rhamnus lanceolata, R. cathartica* and *R. caroliniana* infected *Avena sativa.* Later, in 1912, Arthur (3), using teleutospores from *Calamagrostis canadensis,* infected *Rhamnus alnifolia.*

Again, in 1916 Arthur (4) put teleutospores from *Holcus lanatus* on *Rhamnus cathartica* and *Lepargyraea canadensis,* but obtained no infection. Another collection of teleutospores on *Scolochlea festucacea* was sown on *Lepargyraea canadensis, Eleagnus argentea* and *Rhamnus cathartica,* but no infection resulted on any of these hosts.

Durrell and Melhus (29) tested the susceptibility of *R. alnifolia, R. caroliniana, R. cathartica,* and *R. frangula* in an oat field to teleutospores on *Avena sativa.* They obtained abundant infection on *R. cathartica,* but not on the other three species. In greenhouse trials of the three species only *R. cathartica* and *R. lanceolata* became infected from teleutospores on oats. These preliminary trials confirmed Carleton's (8) and Arthur's (2) results with *R. lanceolata,* altho they did not use teleutospores in their trials. They took the aecidiospores from *R. lanceolata* and obtained crown rust on oats. The field trials by Melhus and Durrell (29) showed that *R. caroliniana, R. frangula* and *R. alnifolia* are less susceptible and probably function as alternate hosts for crown rust on oats less frequently than do *R. cathartica* and *R. lanceolata.* It should be emphasized in passing that to date Arthur is the only American investigator who has attempted to carry crown rust from its grass hosts to American species of Rhamnus and he only made a few trials with crown rust on three species of grasses. This should indicate clearly the necessity of a detailed study of the genus Rhamnus in its

relation to crown rust on many grass hosts in the open and in greenhouse infection trials. The data available as to the distribution of Rhamnus species and prevalence of the infection in the open follow.

DISTRIBUTION OF RHAMNUS SPECIES AND CROWN RUST AECIDIUM

In studying the question of the alternate hosts of crown rust, two points became involved, namely, the distribution of Rhamnus species and the occurrence of the aecidium of crown rust in the open.

Both native and introduced species of Rhamnus are quite widely distributed over the United States. The introduced European species, *Rhamnus frangula* and *R. cathartica*, are for the most part cultivated in the northern sections of the United States. *Rhamnus frangula* is used as a hedge and ornamental plant in the eastern and northern United States. It has escaped in boggy places on Long Island, northern New Jersey, and Ontario, Canada, according to Britton (6). The aecidium of crown rust on *R. frangula* is probably rare in the middle west. *Rhamnus cathartica* is native in northern Asia and thus adapted to a cool climate. In the United States it is found growing commonly thruout the middle and the northwestern states as an ornamental shrub or hedge plant. Even tho an introduced species, *R. cathartica* has escaped from cultivation in many places. Noteworthy examples have been found in Wisconsin, Minnesota, South Dakota, Illinois and Iowa. This situation is important from an economic standpoint, especially where hedges occur about farmsteads or oat fields.

Observations in regard to the role of *R. cathartica* in the distribution of crown rust to oats have been made by the writers at the following places: Iowa: Clarion and Hinton; Wisconsin: Madison, Janesville, Avalon, Emerald Grove and vicinity of Delavan lake; Illinois: Antioch; Minnesota: Warren. In each instance the *R. cathartica* shrubs had escaped from cultivation and were growing as hedges either bordering an oat field or not more than a half mile distant. It was evident from the amount of early aecidial infection that these shrubs acted as a medium for distribution of the crown rust. Such local areas proved to be centers for a serious epidemic. At Hinton, Iowa, where a farm of 80 acres was surrounded with a 40 year old *R. cathartica* hedge, a serious epidemic developed in 1920 and 1921. In 1921, 40 acres of oats surrounded on three sides by this hedge were entirely killed, while fields on adjoining farms were also very seriously injured. Crown rust spread over a large area, extending 15 miles in a westerly direction, before crown rust was found elsewhere in the state. In this connection it is interesting to note that Henning (18) in Denmark recently called attention to the fact that *R. cathartica* should not be cultivated because of its economic importance in the distribution of crown rust on oats.

The distribution of our native species of Rhamnus in North America is not well understood, nor is the question of species well defined. Greene (14), (15), (16), (17), has described ten new species native to United States and Rose (35), five in Mexico and Central America. For the most part, the following species of Rhamnus described by Greene are found in the western and southwestern parts of the United States: *R. fasciculata, R. ursina, R. castorea, R. cuspidata, R. obtusissima, R. pirifolia, R. betulaefolia, R. anonaefolia, R. rubra,* and *R. smithii.* Of this group, the only species on which aecidium has been collected is the last mentioned, *R. smithii.* The five described by Rose are *R. nelsoni, R. obliqua, R. revoluta, R. pringlei* and *R. discolor.* These groups are confined to regions where oats are little grown, if at all. Thus these species are probably not an active agent in the distribution of the crown rust of oats. The extent to which they serve as alternate hosts for crown rust on the native grasses is not known.

Rhamnus crocea Nutt. is reported to be confined to a comparatively small area, since it is reported only from southern California. *Rhamnus ilicifolia* has been described by Kellogg (23) as a species and by Greene as a variety of *R. crocea.* This species, likewise, is found in middle and southern California. Green also places *R. pilosa* Trelease as a variety of *R. crocea.* No data are at hand regarding a crown rust aecidium on these species. *R. californica* Esch. occurs in abundance on the west coast of California, Oregon and Washington, and frequently is cultivated as an ornamental shrub. Brewer and Watson[1] place *R. tomentella* Greene as a variety of *R. californica.* Howell (20) describes the species *R. occidentalis* from Oregon.

Rhamnus caroliniana Walt. and *R. lanceolata* Pursh. are perhaps the two native species of widest distribution in North America. *R. caroliniana* is a southern species extending eastward from Texas, Kansas and Missouri. It is found on shaded hillsides and stony ridges. It is seldom used for ornamental purposes or hedges, thus its contact with oats is more remote than in the case of *R. cathartica* L. and *R. frangula* L. The crown rust aecidium occurs on *R. caroliniana* Walt. in the field, but has never been found to be an active agent in the distribution of crown rust on oats. In 1905 Arthur (2) reported finding infection on this species in a garden at LaFayette, Indiana. In the spring of 1920, Kurtzweil collected the aecidium on *R. caroliniana,* at Knoxville, Tennessee. *Rhamnus lanceolata* Pursh., like *R. caroliniana* Walt., is most commonly found in moist soil along small streams. It occurs somewhat farther north, extending into Nebraska, Iowa, Illinois and eastward to Pennsylvania and southward to Florida. The aecidial stage occurs annually on *R. lanceolata* in Iowa, Illinois and Missouri. In 1920 a case

[1]Brewer, W. H., and Watson, Sereno, Botany of Calif., **1**:100-101. 1876.

was found at Indianola, Iowa, where a rust survey indicated that the uredospore generation on oats was started by the aecidium from *R. lanceolata.* In 1921, similar data suggested that the uredospore generation on *Festuca pratensis* and *Calamagrostis canadensis* was initiated by the aecidium on *Rhamnus lanceolata.* This plant is not used as an ornamental shrub or hedge plant and therefore seldom grows near oat fields.

R. smithii is found only in the southern Rocky Mountain region, where it occurs abundantly as a native shrub. The aecidium is also abundant and crown rust occurs on several grasses in the immediate vicinity. However, oats are not grown in that region near this Rhamnus species.

Rhamnus alnifolia L'Her. is primarily a northern species, reaching the southern limits of its distribution in northern Iowa, Nebraska and Illinois. It is almost entirely confined to swamps, hillsides and shady banks of streams. The aecidium on this host has been collected and transferred to *Avena sativa* and *Calamagrostis canadensis.* At Sturgeon Bay, Wisconsin, it was evident that the aecidium on *R. alnifolia* was directly responsible for the crown rust infection on *Calamagrostis canadensis.* Here again, due to its habitat, *R. alnifolia* probably does not act as a direct agent in the distribution of crown rust to *Avena sativa,* except in rare cases.

Rhamnus purshiana DC. is a western species, occurring generally on the Pacific coast range thru Washington, Oregon, Idaho, Montana and California. Altho the aecidium of crown rust on this host has frequently been collected in the northwest, its relation to *Avena sativa* is not well understood.

Two other western shrubs, *Lepargyraea canadensis* Greene and *L.argentea,* have been exposed to crown rust infection by Arthur (4) to determine whether or not they were alternate hosts for crown rust. Mr. E. Bethel of Denver, Colorado, has supplied information bearing on the relation of this host to crown rust. However, as yet no cultural work has been attempted to substantiate his field observations. It should be recalled in this connection that an *Aecidium allenii* Clinton on *Lepargyraea canadensis* Greene (*Shepperdia canadensis* Nutt.) has frequently been collected, but the relation of this aecidium to crown rust is not known. Lepargyraea is commonly found in the Rocky Mountain regions. Field observations have been made in Colorado in regard to this shrub, but as yet little cultural work has been done. The latter part of June, 1921, in the vicinity of Lake Eldora, Colorado, *Lepargyraea canadensis* was found to be heavily infected with an aecidium. Immediately surrounding these shrubs the following grasses were growing: *Calamagrostis canadensis, Trisetum subspicatum, Koeleria cristata, Bromus ciliatus* and *Agropyron sp.* Teleutospores were collected and identified as

crown rust. It is not known what relation, if any, this bears to the form of crown rust on oats.

In September, 1921, aecidiospores were collected on *Leparagyraea canadensis* in Estes Park, Colorado. Grasses infected with teleutospores of crown rust growing near these shrubs were *Calamagrostis canadensis, Trisetum subspicatum* and *Bromus ciliatus.* Aecidia were also collected at that time on *Lepargyraea canadensis* at Eldora, Colorado.

METHODS AND MATERIALS

During the past three years, tests have been made in the greenhouse and laboratories at Ames to determine which of the American species of buckthorn are susceptible to crown rust. It has not been possible to obtain all the species native to the United States, but the following were secured and grown in the greenhouse:

Rhamnus alnifolia, from Sturgeon Bay, Wisconsin.
Rhamnus cathartica, from Mt. Arbor Nurseries, Shenandoah, Iowa.
Rhamnus californica, from California.
Rhamnus californica var. *tomentella,* from Niles, California.
Rhamnus caroliniana, from Knoxville, Tennessee.
Rhamnus crocea, from California.
Rhamnus frangula, from Mt. Arbor Nurseries, Shenandoah, Iowa.
Rhamnus lanceolata, from Indianola, Iowa.
Rhamnus purshiana, from California.
Rhamnus smithii, from Boulder, Colorado.

Some of these plants were heeled in during the winter, while others were obtained directly from their native habitat in the spring and planted in the greenhouse. Young and succulent leaves were secured either by severe pruning, or by forcing by means of heat and fertilization.

These shrubs were exposed to infection, using germinating teleutospores from *Avena sativa, Calamagrostis canadensis,* and *Festuca elatior.* The teleutospore material was gathered in the fall and stored during the winter out of doors until the resting period was over in the spring. At this time the Rhamnus species were exposed to infection by placing them in a moist chamber with the straw bearing the teleutospores. The plants, straw, and the sides of the chamber, were then wet by a fine spray. If the chamber showed signs of becoming dry before the close of the incubation period, it was opened and sprayed again. At the end of two days the plants were removed to the greenhouse bench, where they were observed for the appearance of the rust. This method successfully produced infection. In cases where but little spore material was available, the spores were germinated on the straw in moist chambers or petri dishes as described by

Melhus and Durrell (29) and later the sporidia were washed off and sprayed on the buckthorn with an atomizer. Infection was first evident by discolored areas, on which later developed pycnidia and finally aecidia.

In the positive trials on given species, four degrees of infection were distinguished, namely:

1. Necrotic areas, no sporulation.
2. Normal pycnidia, no aecidia.
3. Normal pycnidia and few aecidia.
4. Normal pycnidia and aecidia.

In the studies on Rhamnus infection, the degree of infection is always specified in terms of 1 to 4. The degree of infection, 1, resulted when the germ tube of the sporidium entered the leaf, and caused etiolated light yellow areas, usually surrounding a dead center with no form of sporulation. Infection 2 gave normal pycnidial development, but little or no evidence of aecidial cup formation. Infection 3 showed normal pycnidia and few aecidia. An infection was classified as 4 when profuse normal pycnidia and aecidia formed.

EXPERIMENTAL DATA

In the summary (table I) are presented the results obtained in infection experiments during 1919, 1920 and 1921 with crown rust teleutospores on nine species of Rhamnus. The teleutospore material was from *Avena sativa, Calamagrostis canadensis,* and *Festuca elatior.* A total of 220 trials are recorded, 73 with teleutospore material from *Avena sativa*, 138 from *Calamagrostis canadensis*, and 9 from *Festuca elatior.*

Germinating teleutospores from *Avena sativa* gave infection on all of the eight species of Rhamnus studied. Six of these eight species are native to North America and two are introduced species, *R.cathartica* and *R.frangula.* On three of these species normal aecidia were produced, namely, *R.cathartica, R.lanceolata* and *R.smithii;* while on *R.alnifolia* and *R.californica* only few aecidia developed. Infection did not develop beyond the pycnidial stage on *R.caroliniana, R.purshiana* and *R.frangula.* Altho no aecidia developed on *R.frangula,* the fact that pycnidia could be produced suggests that under certain conditions aecidia containing viable aecidiospores may be developed. These infection trials show that not only *R.cathartica* but also *R.lanceolata, R.smithii R.frangula* and *R.californica* can serve as alternate hosts and initiate primary uredospore infection.

A certain degree of infection with teleutospores from *Calamagrostis canadensis* resulted on all nine species of Rhamnus listed in table II. Normal infection was secured only on five species, namely, *Rhamnus lanceolata, R.smithii, R.alnifolia, R.crocea* and *R.californica.* Only pycnidial development showed on the three species, *R.frangula, R.purshiana* and *R.caroliniana.* In many of

TABLE I. INFECTION EXPERIMENTS ON SPECIES OF RHAMNUS WITH CROWN RUST

Rhamnus species	Teleutospores on	1919						1920						1921					
		Degree infection						Degree infection						Degree infection					
		Trials	None	Flecks	Pycnidia	Few Aecidia	Normal	Trials	None	Flecks	Pycnidia	Few Aecidia	Normal	Trials	None	Flecks	Pycnidia	Few Aecidia	Normal
R.cathartica	A.sativa	5	2				3	11					11						
" "	F.el.	1					1												
" "	C.canad.	9	7			2		5		5			3	6	6				
R.lanceolata	A.sativa	5	2				3	4					4						
" "	F.el.	1					1												
" "	C.canad.	11	2			1	8	4	3	1				6					6
R.smithii	A.sativa	2				2		2					2						
" "	F.el.																		
" "	C.canad.	2	1				1	6					6						
R.alnifolia	A.sativa	5	2			3		4	4										
" "	F.el.	1					1												
" "	C.canad.	7					7	7	2				5						
R.caroliniana	A.sativa	3	1		2			5	4		1								
" "	F.el.																		
" "	C.canad.	5	3		2			4		2	2								
R.californica	A.sativa	4				4		5	3			2							
" "	F.el.	1					1												
" "	C.canad.	7			6		1	4		1	1	2		6				6	
R.cal. tomentella	A.sativa	3	1			2													
" " "	F.el.	2				2													
" " "	C.canad.	4		4										6				6	
R.purshiana	A.sativa	2		2				2	1		1								
" "	F.el.	1	1																
" "	C.canad.	3	2	1				4	2	1	1								
R.frangula	A.sativa	5	2	2	1			6	6										
" "	F.el.	2	2																
" "	C.canad.	11	7	2	2			9	8	1				6	6				
R.crocea	A.sativa																		
" "	F.el.																		
" "	C.canad.													6					6

the trials on the three above mentioned species, only flecking resulted, and under the most favorable conditions obtainable, only pycnidia developed. This does not preclude the possibility of aecidia being produced under certain conditions. Just why pycnidia should form and not aecidia was not obvious from these data.

Teleutospores of crown rust on *Festuca elatior* were only available in limited quantity in 1919. Eight species of Rhamnus were exposed to infection from teleutospores on *Festuca elatior*. Normal infection resulted on four of these species, namely: *R.cathartica*, *R.alnifolia*, *R.lanceolata* and *R.californica*, while no infection was evident on *R.purshiana* and *R.frangula*. These trials suggest that crown rust on *Festuca elatoir* favors much the same alternate hosts as crown rust on *Avena sativa*.

Only the maximum degree of infection is recorded in table II. Here it is obvious that crown rust on the three hosts studied all developed aecidia on *Rhamnus cathartica*, *R.lanceolata*, *R.alni-*

TABLE II. THE COMPARATIVE RESPONSE OF SPECIES OF RHAMNUS TO CROWN RUST ON THREE HOSTS.

Teleutospore hosts	Rhamnus species									
	R.cathartica	*R.lanceolata*	*R.smithii*	*R.alnifolia*	*R.crocea*	*R.californica*	*R.cal. tomentella*	*R.caroliniana*	*R.purshiana*	*R.frangula*
Avena sativa	4	4	3	3		3	3	2	2	2
Calamagrostis canadensis	3	4	4	4	4	4	3	2	2	2
Festuca elatior	4	4		4		4	3		0	0

folia, R.californica. These species of Rhamnus are probably the most widely distributed in North America, excluding *R.caroliniana.* In this connection, it may also be noted that crown rust is generally distributed over the United States on the three teleutospore hosts used. It may well be that the distribution and susceptibility of the four Rhamnus hosts listed above in some way account for the wide distribution of crown rust on *Avena sativa, Calamagrostis canadensis,* and *Festuca elatior.*

Among the Rhamnus hosts there was a difference in susceptibility, even tho all of the above named species developed aecidia. *R.lanceolata* proved to be the most susceptible to crown rust from *Avena sativa, Calamagrostis canadensis,* and *Festuca elatior.* It is one of the most widely distributed native species in North America. The other native species of Rhamnus of wide distribution is *R.caroliniana.* This species, according to laboratory trials and limited evidence of infection on it in the open, is quite resistant to the crown rust occurring on the hosts studied. Altho in the spring of 1919 and 1920 rather extended searches were made for the aecidium, it was only found once, at Knoxville, Tennessee, in 1920. This does not preclude its more common occurrence in some locality which has not been searched. The general distribution of crown rust on *Avena sativa* in that part of the United States where *Rhamnus caroliniana* is prevalent may well be due to crown rust uredospores surviving the winter, or the development of the aecidium on *R.caroliniana* under certain environmental conditions.

II. SPECIALIZATION OF CROWN RUST

Crown rust (*Puccinia coronata* Corda) occurs on oats and a number of native and introduced grasses in the chief oat-growing sections of the United States. In Europe there has been found to exist a marked specialization of the crown rust to certain gramineous hosts by Eriksson (10), Klebahn (24), Mühlethaler (30), (31), and others. In America the question of biological

specialization has received little consideration. It is significant to know the host range of crown rust as it occurs naturally in the open and the relation of crown rust on different hosts to one another. This question has a fundamental bearing on oat breeding for resistance, distribution and destructiveness of crown rust on oats.

The studies in this chapter deal with crown rust on *Avena sativa, Calamagrostis canadensis, Lolium perenne* and *Holcus lanatus*, which seem to be the most common grass hosts for the crown rust in the chief oat growing sections.

That some form of specialization exists is clear from Eriksson's early work. He first definitely recognized specialized forms of crown rust in 1894. He divides these forms into four series, each series including the *"forme species"* which are congenial with certain alternate hosts.

These divisions are as follows:

Series I. Aecidium on *R.cathartica* (*R.elaeoides, R.grandifolia, R.alnifolia.*) (*Puccinia coronifera* Kleb.)
1. f. sp. Avenae on *Avena sativa.*
2. f. sp. Alopecuri on *Alopecurus pratensis.*
3. f. sp. Festucae on *Festuca elatior* (and *F.rubra*).
4. f. sp. Lolii on *Lolium perenne.*

Series II. Aecidium on *Rhamnus frangula*:
(*Puccinia coronata* [Corda] Kleb.)
5. f. sp. Calamagrostis on *Calamagrostis arundinacea,* and *C.lanceolata.*

Series III. Aecidium on *Rhamnus dahurica*:
(*Puccinia coronata* var. *Himalensis* Barcl.)

Series IV. Aecidium unknown.
6. f. sp. Melicae on Melica nutans

Additional research work with the hosts of crown rust by Klebahn (25), (26), (27), (28), and Eriksson (11), (12), resulted in adding new forms to both *Puccinia coronifera* and *P.coronata.*

Series I.	Series II.
P.coronifera Kleb..	*P.coronata* (Corda) Kleb.
Avenae	Calamagrostis
Alopecuri	*Holci
Festucae	Phalaridis
Lolii	Agrostis
Glycereae	Agropyri

Mühlethaler (31), however, from the interpretation of his results arrives at a somewhat altered grouping, adding three forms to series I, as designated by Eriksson, and one new species, *Puccinia alpinae coronata.* He includes only three f. sp. under *P.coronata* (Corda) Kleb. Mühlethaler's arrangement is as follows:

*The f. sp. Holci refers to the biologic form on *Holcus lanatus* (*Notholcus lanatus.*)

1. *Puccinia coronifera* Kleb.
   Aecidien auf Rhamnus—Arten der Gruppe Cervispina und Rh. *Imeretina* hort.
   1. f. sp. *Avenae.*
   2. f. sp. *Alopecuri.*
   3. f. sp. *Festucae,* auf *Festuca elatior, arundinaceae* (Schweiz), *gigantea, varia, alpina.*
   4. f. sp. *Lolii,* auf *Lolium remotum* var. *aristatum, temulentum, perenne, rigidum, italicum, Festuca elatior,* (Schweiz), Von f.sp. *Festucae* in der Schweiz unscharf getrennt.
   5. f. sp. *Glyceriae*
   6. f. sp. *Agropyri*
   7. f. sp. *Epigaei*
   8. f. sp. *Holci*
   9. f. sp. *Bromi,* nov. f. sp., auf *Bromus erectus, erectus* var. *condensatus, inermis, sterilis, tectorum, secalinus, commutatus,* wahrscheinlich auch *asper.*
2. *Puccinia himalensis* (Barcl.) Diet.
   Aecidien auf Rh. dahurica, Teleutosporen auf Brachypodium silvaticum. (Viellecht zu Pucc. coronifera.)
3. *Puccinia Alpinae-coronata* nov. sp.
   Aecidien auf Arten der Gruppe Espina, sowie auf Rh. Purshiana DC. Teleutosporen auf Calamagrostis varia und C.tenella.
4. *Puccinia coronata* (Corda) Kleb.
   Aecidien auf den Gruppen Frangula und Alaternus, sowie auf Rh. Imeretina hort.
   1. f. sp. Calamagrostis.
   2. f. sp. Phalaridis, der f. sp. Calamagrostis gegenüber nicht scharf fixiert.
   3. f. sp. Agrostis.
      Dazu treten wahrscheinlich (nach Eriksson) f. sp. Holci und f. sp. Agropyri.
5. *Puccinia coronata* Corda s. lat.
   f. sp. Melicae. Aecidium unbekannt.

METHODS AND MATERIALS

The methods followed in this study of crown rust are a combination of the technique and devices of other workers, coupled with such modifications as were found necessary during the course of this work. The general method followed in exposing the plants to infection is that worked out by Melhus and Durrell (29) with the exception that the plants were exposed to infection under bell jars in their respective cages rather than all held in the same chamber.

As it was deemed advisable to work with these biologic forms separately, steps were taken to devise a means of keeping them separate and at the same time provide plenty of light and moisture. The benches in the greenhouse ran lengthwise, east and west. The bench on the extreme south side of the wing was divided, by means of muslin partitions, into nine compartments, each 36 inches wide and reaching from the bench to the roof. The sides were the width of the bench, as shown in fig. 1. To provide against any stray spores which might be carried by the air, a strip of cheese cloth was stretched lengthwise across the

Fig. 1. Arrangement of compartments for separate collections of crown rust on side bench in greenhouse.

back, while the front was covered by a curtain of a fine quality of muslin, so made that it could be raised from the bottom. This allowed free access to the cage. When not raised, the curtain was secured by means of fastenings at the sides and bottom. A single biologic form of crown rust was placed in each compartment. The middle of the bench was similarly arranged (fig. 2), it being wide enough to provide a double row of compartments facing opposite directions with two feet of space between the rows. The back was four feet high, while the front was three. These were likewise covered with muslin, including the top of the compartment, the front being covered with muslin curtains, fastened at the bottom. Each form of rust was placed in one of the compartments.

One uredospore generation was produced, after which the culture was propagated from a single pustule. About six or seven days after exposure to infection, and before any of the pustules had broken thru the epidermis, spores from a single pustule were placed on an uninfected seedling plant and kept in a separate compartment until rust appeared, after which it was placed in the original compartment, all old plants were discarded and the compartment disinfected with bichloride of mercury (1-1000). All of the experiments were based upon these single pustule isolations from each form.

The hands and arms of the workers were washed in bichloride of mercury (1-1000), and all the inoculation implements were washed in alcohol (95 percent) after working in each compartment. A plant, after being once placed in a compartment, was discarded if removed. All unexposed plants were kept on benches outside the cages.

The plants were all exposed to infection in the seedling stage and kept from 7 to 14 days. Ten plants were left in each pot. The plants were sprayed with distilled water and gently rubbed between the fingers to remove the bloom. They were again sprayed with distilled water and uredospores applied by means of a small scalpel. The plants were then placed on a plate under a bell jar. If dry, water was placed in the plate. The sides of the jar were also sprayed with water.

Serious difficulties were encountered in the cultural experiments because of the high temperatures that prevailed under glass in the greenhouse during the late spring. This difficulty was partly overcome by a spraying system devised to reduce the temperature. Holes 1 16 inch in diameter were bored at three feet intervals in a 1⅜ inch gas pipe. This was suspended from the roof of the greenhouse, the pipe was turned with the holes upward, one end of the pipe being closed, the other attached by means of a hose to the water tap. When the water was turned on, it struck the roof of the greenhouse with such force that it was broken up into a fine spray. The ventilators in the top were open so as to take care of the excess moisture. This spray fell below on the sloped tops of the compartments in sufficient amount to keep the muslin moist. The evaporation caused the temperature of the whole house to be reduced from above 40°C to 29°C.

The infection obtained was determined in terms of the letters 0, A— and A+, each having the following significance as to degree of infection:

0 = No infection, but sometimes necrotic areas and flecking present.

A— = Infection subnormal, weak, resistant; pustules small to medium in size, usually not rupturing epidermis, surrounded by etiolated areas.

A+ = Infection normal to subnormal; susceptible, pustules medium to large, usually rupturing epidermis; usually no etiolation surrounding sori.

It should be understood that the division of degree of infection into A— and A+ is purely arbitrary, and used to indicate differences that do not readily lend themselves to any other means of expression. The types A— and A+ are not positively fixed, but include a certain amount of variation in degree of infection between the two extremes in each type.

The number of trials made with each host is not indicated in the tabular matter under each biologic form. In no case were there less than six trials and in the majority of cases there were more than 20 and often 30 or more. This was especially true on those hosts giving a 0 or A— degree of infection. A three inch pot containing about ten individual plants is considered a single trial. Some leaves on all of the individual plants were exposed to infection in each trial.

Fig. 2. Arrangement of comparements on middle bench for separating the forms of crown rust.

BIOLOGIC FORM AVENAE

Crown rust occurring on oats (*Avena sativa*) was studied first because of its accessibility, economic importance, and wide distribution. The first collection of crown rust on *Avena sativa* used in these cultural studies was made at Ames in 1918 and maintained in stock culture in the greenhouse until June, 1921. Spores taken from this culture were used in the studies of this biologic form. The results obtained are shown in table III. Those species on which infection followed are arranged in groups in relation to the degree of infection, ranging from 0 to A+, having the value assigned under the discussion on "Method and Materials." The 64 species that were exposed but gave no infection are listed alphabetically in the 0 group.

The biologic form of crown rust occurring on oats seems to be neither highly specialized nor limited to hosts in a single tribe. Species in six of the possible eleven tribes of the Gramineae represented in the United States were infected, at least to some extent. The distribution of the genera and species studied in the tribes are as follows:

Tribes	Infection		No Infection	
	No. Genera	No. Spec.	No. Genera	No. Spec.
Avenae	4	7	2	3
Agrostideae	4	5	6	8
Andropogoneae	0	0	0	2
Chlorideae	1	1	2	3
Festuceae	5	7	7	24
Hordeae	1	2	7	19
Phalarideae	1	1	1	1
Paniceae	0	0	2	4
Total	16	23	28	64

Normal infection, A+, occurred only on nine species in five genera, which are as follows: *Avena sativa, A.fatua, A.sterilis, Anthoxanthum odoratum, Alopecurus pratensis, Festuca octo-*

TABLE III. HOST RANGE OF BIOLOGIC FORM AVENAE.

Biologic Form	Hosts		Degree Infection
Avena sativa	*Avena sativa* *Avena fatua* *Avena sterilis* *Anthoxanthum odoratum* *Alopecurus pratensis* *Festuca octoflora* *Arrhenatherum elatius* *Alopecurus geniculatus* *Avena barbata*		A+
	Peckmannia erucaeformis *Dactylis glomerata* *Festuca confinis* *Lolium perenne* *Lolium temultentum* *Puccinellia airoides* *Polypogon monspeliensis* *Sporobolus cryptandrus* *Bromus polyanthus* *Festuca gigantea* *Holcus lanatus* *Molinia coerulea* *Phleum pratense* *Sphenopholis obtusata*		A−
	Agropyron caninum *Agropyron desertorum* *Agropyron pseudo-repens* *Agropyron repens* *Agropyron Richardsonii* *Agropyron Smithii* *Agropyron tenerum* *Agrostis alba* *Andropogon provincialis* *Andropogon scoparius* *Asprella hystrix* *Bouteloua curtipendula* *Bouteloua oligostachya* *Bromus arvensis* *Bromus brizaeformis* *Bromus ciliatus* *Bromus inermis* *Bromus japonicus* *Bromus Kalmii* *Bromus marginatus* *Bromus secalinus* *Bromus tectorum* *Calamagrostis canadensis* *Calamovilfa longifolia* *Danthonia spicata* *Deschampsia caespitosa* *Deschampsia flexuosa* *Elymus canadensis* *Elymus Macounii* *Elymus robustus* *Elymus striatus* *Elymus virginicus* *Eragrostis pectinacea* *Festuca arundinacea* *Festuca nutans* *Festuca ovina* *Festuca pratensis* *Festuca rubra*	*Glyceria fluitans* *Glyceria grandis* *Glyceria nervata* *Hordeum jubatum* *Hordeum Pammeli* *Hordeum vulgare* *Koeleria cristata* *Lolium Italicum* *Melica nutans* *Muhlenbergia mexicana* *Panicum autumnale* *Panicum crusgalli* *Panicum virgatum* *Paspalum sanguinale* *Phalaris arundinacea* *Poa flava* *Poa palustris* *Poa pratensis* *Poa trivialis* *Secale cereale* *Spartina cynosuroides* *Sporobolus asper* *Sporobolus cuspidatus* *Sporobolus heterolepis* *Stipa spartea* *Triticum vulgare*	0

flora, Arrhenatherum elatius, Alopecurus geniculatus, and *Avena barbata.* The last three species were not as readily infected as the first six. Under the most favorable conditions, for both the host and parasite, that could be provided under glass, 14 other species showed only a subnormal infection. Normal infection may develop on these grasses in the open under certain conditions, thus it would not be safe to exclude them from this form.

It is not improbable that further infection experiments will show that the number of susceptible species can be increased. This is borne out by the data submitted by Carleton (7) and others. Carleton succeeded in producing infection on three species of grass, *Phalaris arundinacea, Koeleria cristata* and *Deschampsia caespitosa,* which in these studies never gave infection. However, he fails to state the degree of infection obtained. Carleton also got positive infection on *Hordeum murinum, Holcus mollis, Alopecurus alpestri, Trisetum subspicatum, Phleum asperum. Poa annua,* and *Ammophila arenaria.* These hosts were not used in these studies. Freeman and Johnson (13) report transferring crown rust to *Hordeum vulgare.* Treboux (36), (37) was also able to infect *Hordeum vulgare* as well as *Agropyron repens. Bromus inermis, B.secalinus, Secale cereale* and *Triticum vulgare* with uredospores from *Avena sativa.* All of these hosts were used in our infection studies, but no infection was obtained. In view of the data at hand, there can be little doubt about the wide host range of crown rust on *Avena sativa* and it seems equally clear that the degree of infection secured is not fixed, but depends upon external and internal conditions of host and parasite. Only two of nine species on which normal infection developed are cultivated plants besides *Avena sativa,* namely: *Arrhenatherum elatius, Alopecurus pratensis.* The other hosts are wild grasses that are common in the northern Mississippi Valley, the chief oat growing section of the United States. Their relation to the overwintering and dissemination of crown rust on oats remains for subsequent study. That they may well have an important relation to crown rust development on oats is possible.

BIOLOGIC FORM LOLII

Crown rust is common on *Lolium perenne* on the Pacific coast, California, Oregon and Washington. The relation of the form on Lolium to the development of crown rust on species of Avena, both wild and cultivated, was unknown. This fact made it seem worth while to investigate its host range and possible specialization.

The crown rust material used in studying this form was collected on *Lolium perenne* at Davis, California, by W. W. Mackie, April 21, 1921. This collection was maintained in stock culture on Lolium thruout the infection trials reported in this paper.

TABLE IV. THE HOST RANGE OF THE BIOLOGIC FORM LOLII

Biologic Form	Hosts	Degree Infection
Lolium perenne	*Anthoxanthum odoratum* *Beckmannia erucaeformis* *Dactylis glomerata* *Festuca arundinacea* *Festuca nutans* *Festuca pratensis* *Festuca rubra* *Lolium Italicum* *Lolium perenne* *Molinia coerulea* *Phalaris arundinacea* *Avena sativa* *Festuca ovina duriuscula*	A+
	Sphenopholis obtusata *Glyceria nervata* *Melica mutica* *Phleum pratense* *Puccinellia airoides*	A−
	Agropyron caninum *Agropyron repens* *Agropyron Richardsonii* *Agrostis alba* *Asperella hystrix* *Alopecurus pratensis* *Arrhenatherum elatius* *Danthonia spicata* *Elymus robustus* *Eragrostis pectinacea* *Festuca confinis* *Festuca dumetorum* *Holcus lanatus* *Poa compressa* *Polypogon monspeliensis*	0

Thirty-three species were exposed to infection; 18 became infected, while 15 remained free from infection as shown in table IV.

The distribution of the species studied in tribes and genera is as follows:

Tribes	Infection		No Infection	
	No. Genera	No. Spec.	No. Genera	No. Spec.
Aveneae	2	2	3	3
Agrostideae	1	1	3	3
Chlorideae	1	1	0	0
Festuceae	6	10	3	4
Hordeae	1	2	3	5
Phalarideae	2	2	0	0
Total	13	18	12	15

Those species that became infected belong in 6 tribes and 13 genera. The largest number of species infected belong in the tribe Festuceae. The degree of infection was normal (A+) on 12 species in 8 different genera. This is a wider host range than in the form Avenae. *Avena sativa* developed an infection slightly below normal after many trials. It is interesting to note that after *A.sativa* becomes infected under greenhouse conditions the crown rust can be maintained on this host indefinitely, show-

ing that under favorable conditions crown rust on *Lolium perenne* may use species of Avena as hosts. Crown rust on *Avena sativa* only gave an infection of A— on *Lolium perenne,* which tends to show that coming the other way was not as easily accomplished. However, both became infected and the difference was merely one of degree. Altho the two hosts in question have been exposed many times, yet it may well be that further trials under different conditions would give an infection of A+ on both hosts. In other words, the division lines between the forms Avenae and Lolii are not marked and it may be that they are one and the same form. For the time being the form Lolii is separated from the form Avenae, but it is not improbable that further work will throw them together.

BIOLOGIC FORM CALAMAGROSTIS

The second most common host of crown rust is *Calamagrostis canadensis.* This fact made it seem worth while to study its host range. The uredospore collection used in this study was made September 15, 1919, at Sturgeon Bay, Wisconsin, by Florence Willey, and maintained in stock culture during the progress of these studies. Table V shows different species in 23 genera of Gramineae that were exposed to infection with uredospores from this collection on *C.canadensis* Seventeen of these species gave

TABLE V. HOST RANGE OF BIOLOGIC FORM CALAMAGROSTIS

Biologic Form	Hosts	Degree Infection
	Calamgrostis canadensis *Calamovilfa longifolia*	A+
Calamagrostis canadensis	*Anthoxanthum odoratum* *Beckmannia erucaeformis* *Festuca pratensis* *Festuca gigantea* *Holcus lanatus* *Lolium perenne* *Agropyron caninum* *Agropyron repens* *Agropyron richardsonii* *Arrhenatherum elatius* *Avena sativa* *Dactylis glomerata* *Phalaris canariensis* *Polypogon monspeliensis* *Sphenopholis obtusata*	A—
	Agropyron desertorum *Agropyron tenerum* *Danthonia spicata* *Deschampsia flexuosa* *Elymus robustus* *Eragrostis pectinacea* *Festuca arundinacea* *Festuca confinis* *Festuca nutans* *Festuca rubra* *Phalaris arundinacea* *Phleum pratense* *Puccinellia airoides*	0

varying degrees of infection, ranging from A— to A+. Normal infection (A+) only occurred on one host plant, *C.canadensis*. After many trials *Calamovilfa longifolia* gave a degree of infection slightly below normal and the remaining 15 species never showed more than a subnormal infection of A—. The distribution of the species of Gramineae into tribes is as follows:

Tribes	Infection		No Infection	
	No. Genera	No. Spec.	No. Genera	No. Spec.
Aveneae	4	4	2	2
Agrostideae	3	3	1	1
Chlorideae	1	1	0	0
Festuceae	2	3	3	6
Hordeae	2	4	2	3
Phalarideae	2	2	1	1
Totals	14	17	9	13

The susceptible hosts do not seem to be limited to a small number of tribes, but are distributed in six. It was never possible to produce normal infection on *Avena sativa*, which suggests a marked difference in the specialization in the crown rusts on *Avena sativa* and *Calamagrostis canadensis*. This specialization is indicated not only on *Avena sativa*, but also on *Anthoxanthum odoratum* and *Arrhenatherum elatius*. Crown rust on *Avena sativa* on these two hosts gave normal infection, while on Calamagrostis only a subnormal infection developed, A—. If crown rust on *C.canadensis* is a distinct form from the form Avenae, it is a case where two forms may under certain conditions use the same hosts. The host range of these two biologic forms is not sharply fixed, but rather plastic and variable, depending upon internal and external conditions of host and parasite.

BIOLOGIC FORM HOLCI

Another common host of crown rust is on *Holcus lanatus*. Its specialization has been considered in the same way as crown rust on *Avena sativa* and *Calamagrostis canadensis*. Two uredospore collections were made, one by Godfrey Hoerner on April 5, 1919, near Portland, Oregon, and another at Bridgeport, Long Island, August 1, 1919, by I. E. Melhus and H. S. Jackson. These two collections were held in stock culture and compared morphologically and physiologically on the 33 grass hosts listed in table VI. As far as could be ascertained, these two collections proved to be alike. In view of this fact, these two collections will be considered hereafter as one collection.

Table VI shows 33 different grass hosts that were exposed to infection with only six species becoming infected. *Holcus lanatus* was the only host on which normal infection developed. Three species of Avena gave a subnormal infection (A—) in less than one-fourth of the trials. Flecking was frequently obtained,

TABLE VI. THE HOST RANGE OF THE BIOLOGIC FORM HOLCI.

Biologic Form	Hosts	Degree Infection
Holcus lanatus	*Holcus lanatus*	A+
	Avena sativa *Avena barbata* *Avena fatua* *Anthoxanthum odoratum* *Phleum pratense*	A−
	Agropyron caninum *Agropyron repens* *Agropyron Richardsonii* *Agropyron Smithii* *Agrostis alba* *Alopecurus pratensis* *Arrhenatherum elatius* *Beckmannia erucaeformis* *Bromus arvensis* *Bromus inermis* *Bromus tectorum* *Danthonia spicata* *Deschampsia flexuosa* *Dactylis glomerata* *Eragrostis pectinacea* *Festuca confinis* *Festuca pratensis* *Glyceria nervata* *Lolium italicum* *Lolium perenne* *Melica mutica* *Molinia coerulea* *Phalaris arundinacea* *Poa compressa* *Poa pratensis* *Polypogon monspeliensis* *Sphenopholis obtusata*	0

but sporulation was rarely secured. *Anthoxanthum odoratum* and *Phleum pratense* were less susceptible than the species of Avena. The distribution of the species of grasses used in the tribes of Gramineae is as follows:

Tribes	Infection		No Infection	
	No. Genera	No. Spec.	No. Genera	No. Spec.
Aveneae	2	4	4	4
Agrostideae	1	1	3	3
Chlorideae	0	0	1	1
Festuceae	0	0	8	12
Hordeae	0	0	3	6
Phalarideae	1	1	1	1
Total	4	6	20	27
Total No. species tried				33

The number of species studied is too limited to warrant a suggestion as to preference of any particular tribe. However, a sufficient number of species of grasses have been studied to indicate that crown rust on Holcus is quite specialized and that the species of Avena tried are very resistant.

DISCUSSION

De Bary (5) in 1865 showed that crown rust (*Puccinia coronata* Corda) was heteroecious and published the data the following year. He sowed the sporidia of crown rust on cut leaves of *Rhamnus frangula* and *R.cathartica* and observed penetration of the germ tube in both cases. He describes his results as follows:

> Die Sporidienkeime drangen ein in die Epidermis von *Rhamnus Frangula* und *cathartica*, zumal in noch nicht völlig erwachzene Blätter derselben; an keiner der übrigen Pflanzen wurde eine Spur von Eindringen beobachtet. Hiermit war im Grunde schon eine ziemlich bestimmte Antwort auf die gestellte Frage gewonnen, denn alle früheren untersuchungen ergeben, dass bei den Puccinien mit überwinternden Teleutosporen die Sporidienkeime immer in die Species eindringen, in welcher sich das Aecidium entwickelt.

In other experiments that de Bary (5) made in the open with crown rust, pycnidia and mature aecidia were produced on *Rhamnus frangula*. The source of the teleutospore material is not stated. The significant point in de Bary's studies is his observation of sporidial germ tube penetration into the leaves of both *R.cathartica* and *R.frangula*. Up to the present writing this finding of de Bary has not been confirmed and has led to the separation of *Puccinia coronata* Corda into two different species and four subdivisions. This separation is based largely on the groups of Rhamnus species which are susceptible to infection. The data presented earlier in this paper show that the sporidia of *Puccinia coronata* Corda on two hosts, *Avena sativa* and *Calamagrostis canadensis*, may enter the leaves of *R.frangula* and at times develop pycnidia. Necrotic areas followed infection more often than pycnidial formations, as indicated in table I. There can be no doubt as to the germ tube penetrating the leaf tissue as described by de Bary. When we consider that necrotic areas and pycnidia may sometimes result from sowing teleutospores on *R.frangula* leaves, it is quite probable that sometimes the development of the crown rust organism may advance further and form aecidia and aecidiospores. As indicated earlier in this paper the difference between necrotic areas, pycnidia and aecidia formation is merely a difference in the degree of development of the rust organism. In the 36 infection trials, using teleutospores from *Avena sativa* and *Calamagrostis canadensis* on *R.frangula*, five gave necrotic areas and three pycnidia. This evidence suggests little justification for the separation of crown rust into different species, according to Klebahn (24), Eriksson (10), and Mühlethaler (30), (31), in Europe. Their failure to obtain positive infection on *R.frangula* with crown rust teleutospores on *Avena sativa* indicates that either an insufficient number of trials was made or crown rust in Europe is different in its response.

Plowright (33) in 1889 first suggests the splitting of *Puccinia coronata* Corda into two species, based on the following inoculation experiments described by him: "I have found, by numerous cultures, that the teleutospores from *Dactylis glomerata* and *Festuca sylvatica* readily produced the aecidium on *R.frangula*, but I have failed to produce on *R.frangula* the aecidium from the teleutospores on *Lolium perenne*. I think two species are confounded under the name of P.coronata."

Klebahn in 1892 confirmed Plowright's findings as to the alternate host of crown rust on *Lolium perenne*. He was able to infect *R.cathartica*, but not *R.frangula*. This evidence coupled with previous infection experiments by Nielsen (32), Cornu (9) and Plowright (33), led him to separate *Puccinia coronifera* from *Puccinia coronata* Corda.

In 1894 Klebahn (25) carried on further infection experiments with teleutospores of crown rust on *R.cathartica* and *R.frangula*. He obtained infection on *R.frangula* with teleutospores from *Calamagrostis arundinacea*, but not on *Rhamnus cathartica*. Teleutospores from *Arrhenatherum elatius* and *Lolium perenne* produced infection on *R.cathartica* but not on *R.frangula*. He did not use crown rust teleutospores from *Avena sativa*. In 1893 Eriksson (10), however, tried teleutospores from *Avena sativa* on both *R.cathartica* and *R.frangula* but obtained infection only on the first named species. In 1911 Mühlethaler (31) attempted to produce infection on *R.frangula* with crown rust teleutospores on *Avena sativa*. The results were again negative. This apparent immunity of *R.frangula* to infection with crown rust from *Avena sativa, Lolium perenne, Arrhenatherum elatius, Festuca arundinacea* and *Bromus erectus* led Klebahn, Eriksson and Mühlethaler to consider crown rust to consist of more than one species. However, when we consider that Treboux (36), (37), was able to take aecidiospores from *R.frangula* and produce uredospores on *Avena sativa*, coupled with the data presented in this paper, showing in 36 trials on *R.frangula* five gave necrotic areas and three pycnidia, it is extremely doubtful whether the separation of crown rust into different species is justifiable.

Treboux (37) also found that the acidiospores from *R.cathartica* infected *Agrostis stolonifera, Calamagrostis arundinacea* and *Phalaris arundinacea*, all of which are listed as hosts for *Puccinia coronata* by Klebahn and Mühlethaler. On the other hand, in localities where only *R.frangula* occurs, two of the hosts of *Puccinia coronifera* were infected with *P.coronata*, namely, *Agrostis alba* and *Poa pratensis*. In the light of his inoculation experiments, using uredospores and aecidiospores, Treboux (37) concludes that the existence of sharply marked biological forms having their aecidial stages on either *R.cathartica* and *R.frangula* is doubtful.

By referring to table II it is clear that all of the native and the two introduced species of Rhamnus studied may be alternate hosts for crown rust occurring on *Avena sativa* and *Calamagrostis canadensis*. Altho the susceptibility of the alternate hosts varies markedly, none is immune.

The degree of susceptibility is probably determined by inherent differences of the Rhamnus species. *Rhamnus lanceolata* is more like *R.cathartica* than *R.frangula*. The same is true of *R.alnifolia*, *R.smithii* and *R.californica*. Those species of Rhamnus that most closely resemble in apearance *R.frangula*, namely: *R.purshiana* and *R.caroliniana*, are likewise most resistant.

Not only do the inherent differences in species of Rhamnus influence their susceptibility, but this susceptibility is also affected by the selective development of biologic forms of crown rust. Crown rust on *Avena sativa* prefers *R.cathartica* and *R.lanceolata* as its alternate hosts. *Puccinia coronata* on *Calamagrostis canadensis*, another biologic form, seems to be less specialized. It produces normal aecidia on five different species of Rhamnus, *R.lanceolata*, *R.alnifolia*, *R.smithii*, *R.californica*, and *R.crocea*. The two biologic forms mentioned above have one Rhamnus host in common on which the normal infection developed, namely: *R.lanceolata*. In the case of the other species of Rhamnus, there occurs marked overlapping, namely, both forms using the same Rhamnus species. In other words, the biologic forms are not fixed as to their alternate host any more than in the case of the uredospore generation on grasses.

SUMMARY

Crown rust (*Puccinia coronata* Corda) on oats (*Avena sativa*) and *Calamagrostis canadensis* may use all of the American species of Rhamnus as alternate host plants. It also may use the two introduced species, *R.cathartica* and *R.frangula*.

There are described in the United States at least seven different native species of Rhamnus, *R.lanceolata*, *R.alnifolia*, *R.caroliniana*, *R.cathartica*, *R.californica*, *R.frangula* and *R.purshiana*. Five of these have a wide distribution, namely: *R.cathartica*, *R.lanceolata*, *R.caroliniana*, *R.purshiana* and *R.frangula*. *Rhamnus caroliniana* is a southern species, occurring on rough, rocky hilltops and along streams. *R.lanceolata* is also southern in its distribution, but extends further north than *R.caroliniana*, northern Iowa being about its northern limit. *R.lanceolata* occurs on hillsides and along small streams, usually at some distance from tillable lands.

The separation of *Puccinia cononata* Corda into two species, *Puccinia coronata* Corda and *P.coronifera*, by Klebahn (27) and these two species into four series by Eriksson (10), based on the

species of Rhamnus used as alternate hosts, is not justifiable in America. Not all species of Rhamnus are equally susceptible to the aecidial stage. The biologic forms occurring on *Avena sativa, Calamagrostis canadensis* and *Festuca elatior* prefer those species of Rhamnus most like *R.cathartica.*

Crown rust on *Avena sativa* produced normal aecidia on *R.cathartica* and *R.lanceolata* and these alternate hosts may serve as important agents in the spread of crown rust on oats. The most dangerous species of Rhamnus to oat growing are the native species, *R.lanceolata,* and the introduced species, *R.cathartica.*

The four most common grass hosts for crown rust in the oat growing sections of United States are: *Avena sativa, Calamagrostis canadensis, Lolium perenne* and *Holcus lanatus.*

The form of crown rust (*Puccinia coronata* Corda) on *Avena sativa* is neither highly specialized nor limited in its host range. Species in six tribes of Gramineae were susceptible. This represents 16 genera, viz., Avena, Anthoxanthum, Alopecurus, Festuca, Arrhenatherum, Beckmannia, Dactylis, Lolium, Puccinellia, Polypogon, Sporobolus, Bromus, Holcus, Molinia, Phleum, Sphenopholis. Normal infection resulted on *Avena sativa, A. fatua. A.sterilis, Anthoxanthum odoratum, Alopecurus pratensis* and *Festuca octoflora.*

The form of crown rust on *Calamagrostis canadensis* was found to have susceptible hosts in fourteen genera in six tribes. The genera are as follows, Calamagrostis, Calamovilfa, Anthoxanthum, Beckmannia, Festuca, Holcus, Lolium, Agropyron, Arrhenatherum, Avena, Dactylis, Phalaris, Polypogon, and Sphenopholis. The infection on the following grasses was normal, *Calamagrostis canadensis* and *Calamovilfa longifolia.*

The host range of crown rust on Lolium is represented in 13 genera, Anthoxanthum, Beckmannia, Dactylis, Festuca, Lolium, Molinia, Phalaris, Avena, Sphenopholis, Glyceria, Melica, Phleum, Puccinellia. Of the grasses exposed to infection with this form, the following gave normal infection, *Anthoxanthum odoratum, Beckmannia erucaeformis, Dactylis glomerata, Festuca arundinacea, F.nutans, F.pratensis, F.rubra, Lolium italicum, L.perenne, Molinia coerulea* and *Phalaris arundinacea.* The crown rust on Lolium may be the same form that occurs on *Avena sativa.*

From results here presented, crown rust on Holcus is more highly specialized as to host range than the other forms studied. Holcus was the only grass becoming normally infected.

The forms of crown rust on Avena, Calamagrostis, Lolium and Holcus may under certain conditions use the same hosts but manifest different degrees of infection.

Avena sativa was a common host, with varying degrees of infection for all the forms of crown rust studied.

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